Variation in *Serripes groenlandicus* (Bivalvia) growth in a Norwegian high-Arctic fjord: Evidence for local- and large-scale climatic forcing

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Abstract

We examined the growth rate of the circumpolar Greenland Cockle (*Serripes groenlandicus*) over a period of 20 years (1983-2002) from Rijpfjord, a high-Arctic fjord in northeast Svalbard (80º 10´ N, 22° 15´ E). This period encompassed different phases of large-scale climatic oscillations with accompanying variations in local physical variables (temperature, atmospheric pressure, precipitation, sea ice cover), allowing us to analyze the linkage between growth rate, climatic oscillations, and their local physical and biological manifestations. Standard Growth Index (SGI), an ontogenetically-adjusted measure of annual growth, ranged from a low of 0.27 in 2002 up to 2.46 in 1996. Interannual variation in growth corresponded to the Arctic Climate Regime Index (ACRI), with high growth rates during the positive ACRI phase characterized by cyclonic ocean circulation and a warmer and wetter climate. Growth rates were influenced by local manifestations of the ACRI: positively correlated with precipitation and to a lesser extent negatively correlated with atmospheric pressure. A multiple regression model explains 65% of the variability in growth rate by the ACRI and precipitation at the nearest meteorological station. There were, however, complexities in the relationship between growth and physical variables, including an apparent 1-year lag between physical forcing changes and biological response. Also, when the last 4 years of poor growth are excluded, there is a very strong negative correlation with ice cover on a pan-arctic scale. Our results suggest that bivalves, as sentinels of climate change on multi-decadal scales, are sensitive to environmental variations associated with large-scale changes in climate, but that the effects will be determined by changes in environmental parameters regulating marine production and food availability on a local scale.

Introduction

The Arctic climate has changed dramatically in the last several decades (Maxwell, 1997; Overpeck *et al.*, 1997, Johannessen *et al.*, 2003, 2004; AICA 2004). The average annual air temperature has increased by 1º to 4º C in the last half century (AICA 2004), and this has been accompanied by changes in terrestrial and marine ecosystems (Oechel & Vorulitis, 1997; Serreze *et al.*, 2000; Morison *et al.*, 2000). Effects of persistent climate change on Arctic marine ecosystems are largely undetermined, but changes that occur in response to decadal-scale climate oscillations may provide insight into longer term effects of more persistent climate change.

Several large-scale climate oscillations have been shown to influence marine systems (see Allan *et al.*, 1996; Ottersen *et al.*, 2001; Walther *et al.*, 2002; Stenseth *et al.*, 2003 for reviews). Linkages between the two climate oscillations with nodes centered in the Arctic, the Arctic Oscillation (AO) and the Arctic Climate Regime Index (ACRI), and the marine ecosystem, however, have not been demonstrated. Both indices reflect differences in wind-driven motion in the central Arctic alternating between two phases, an anticyclonic circulation regime (ACCR) and a cyclonic circulation regime (CCR). The climate regimes manifest as physical variables in the Arctic; ACCR is characterized by a cold and dry high-Arctic atmosphere and a colder and saltier polar ocean (low AO and negative ACRI), whereas the cyclonic regime is characterized by a warm and wet atmosphere and a warm and fresh polar ocean (high AO, positive ACRI). Climatic conditions associated with both the AO and ACRI may affect marine ecosystems as has been demonstrated for the North Atlantic Oscillation (Ottersen *et al*. 2001).

Seafloor communities may be the best location to examine the impact of Arctic climate oscillations, and by extension the potential effects of climate change on the Arctic ecosystem. There is often a close relationship between water column and benthic processes (Grebmeier *et al.*, 1988; Ambrose & Renaud, 1995; Piepenburg *et al.*, 1997; Wollenburg & Kuhnt, 2000; Dunton *et al*. 2005), and therefore long lived, sessile benthic organisms, may be more appropriate monitors of climate change (e.g. Kröncke *et al.*, 1998, 2001; Dunton *et al.* 2005) than the more transient pelagic system. Additionally, benthic communities are key components in the carbon cycle on Arctic shelves (Grebmeier *et al*., 1989, Stein & Macdonald, 2004; Grant *et al.*, 2002; Clough *et al.*, 2005) and food for higher trophic levels (e.g. bottom feeding fish, mammals, and birds (Dayton, 1990)). Consequently, changes to the benthos may have profound effects on carbon cycling, trophic structure, and food web dynamics on Arctic shelves.

Bivalves comprise a significant proportion of the benthic biomass of Arctic shelves (Zenkevitch, 1963; McDonald *et al*., 1981; Feder *et al*., 1994; Gulliksen *et al.*, 1985; Grebmeier *et al.*, 1988; Dayton, 1990). The shells of most bivalves exhibit periodic banding, or growth lines (Rhodes & Penella, 1970; Clark, 1974; Rhoads & Lutz, 1980), that have proved valuable in developing a history of environmental change in marine systems (Andrews, 1972; Hudson *et al.*, 1976; Jones, 1981; Jones *et al.*, 1989; Witbaard, 1996; Witbaard *et al.*, 1997, 1999; Tallqvist & Sundet, 2000; Schöne 2003; Müeller-Lupp & Bauch 2005). Temperature and food are the two main factors influencing bivalve growth (Buekema *et al.*, 1985; Beukema & Cadée, 1991; Jones *et al.*, 1989; Lewis & Cerrato, 1997; Dekker & Beukema, 1999; Witbaard *et al.*, 1997, 1999; Schöne *et al*., 2005), and both are likely to be influenced by climate change in Arctic marine systems (Carroll &

Carroll, 2003). Furthermore, many deep water and high latitude bivalves have life spans of decades (Tallqvist & Sundet, 2000; Müeller-Lupp *et al.*, 2003; Sejr & Christensen, 2006) to well over 100 years (Turekian *et al.*, 1975; Thomson *et al.*, 1980; Zolotarev, 1980, Peck & Bullough, 1993; Witbaard *et al.*, 1999, Sejr *et al*., 2004). Bivalves can thus serve as bioproxies by providing uninterrupted records of environmental conditions over decades to centuries, which is critical in the Arctic given the paucity of long term data on community structure and dynamics.

We examined interannual variation in growth of the circumpolar Greenland Cockle (*Serripes groenlandicus*) from 1983-2002 in a high-Arctic fjord in northeast Svalbard (Norwegian Arctic) to explore the relationship between benthic communities and environmental variations associated with decadal climate oscillations in the Arctic. Variation in bivalve growth associated with changes in environmental conditions that occur over the course of a decadal-scale oscillation cycle provides insight into the response of a dominant member of the Arctic benthos to predicted long-term climate change.

Materials and Methods

Study Site

Rijpfjord (80° 10′ N, 22° 15′ E) is located on the north-central shore of Nordaustlandet (Fig. 1), north and east of Spitsbergen in the Svalbard Archipelago. Rijpfjord is oriented south-north and opens to a broad shallow shelf of approximately 200m depth extending to the shelf-break of the Polar Basin at roughly 81° N. The bottom depth averages 200-250m, but an irregular sill crosses the width of the fjord midway through its length. Shallower depths are dominated by bedrock and stones covered with a thin layer of mud, while soft sediments predominate deeper sections.

Rijpfjord is a true polar fjord. It is predominately ice-covered for at least 9 months a year (October-June), with breakup occurring between mid-July and mid-August. Even during the summer period, winds often force drifting pack ice into the fjord. The shallow outlet of the Rijpfjord shelf to the Polar Ocean results in little warm Atlantic subsurface water entering the fjord from the north (Sundfjord, unpub. data). The upper 10 m is a mixed layer with surface water of lower salinity and higher temperature associated with sea ice melt and *in situ* radiative warming; below which is a water mass with a temperature consistently < -1°C and a salinity > 33 ‰ (Fig. 2).

Bivalve Collection

Divers collected four *Serripes groenlandicus* individuals from 17 m depth on 28 August 2003. Individuals were identified by their pale, white siphon, and were dug from the sediment where they were buried to a depth of 5 cm. All animals were alive at the time of collection. Soft tissues were immediately separated from the shells, and the shells air dried.

Strontium/Calcium Ratios

S. groenlandicus deposit distinctive lines during growth which appear as alternating thin dark and thicker light bands on the external shell surface. We used changes in the ratio of Strontium to Calcium in different areas of the shell to identify whether external lines were deposited annually. The Sr/Ca ratio in carbonate varies with the water temperature at the time of deposition (Zacherl *et al.*, 2003; Bath *et al.*, 2004), so systematic changes between presumptive growth lines, reflecting seasonal changes in water temperature, would suggest the lines are deposited annually. We measured Sr/Ca ratios along the growth axis within the prismatic layer of two *S. groenlandicus* shells (N1 and N3) using a

New Wave Research UP213 laser ablation system coupled to a Thermo Finnigan *Element2* single collector sector field ICP-MS. The valves were mounted in resin and a 10mm cross section was cut along the axis of maximum growth using a low-speed saw equipped with a diamond blade. The section was mounted on a petrographic slide with cyanoacrylic glue, polished using 30μm and 3 μm Al_2O_3 lapping film, and then decontaminated in a clean room. Each valve was scrubbed with a nylon brush, triple rinsing with 2% HNO_3, sonicated for 5 minutes in ultra pure H_2O, triple-rinsed in water, and then dried for at least 24 hrs under a laminar flow clean bench.

Instrument set-up was similar to that outlined by Günther & Heinrich (1999) as modified by Thorrold *et al*. (2001). Linear spatial resolution was 100 μm along the growth axis which corresponded to weekly resolution during early years of life, declining to monthly resolution as shell growth rates decreased at older ages. Quantification of Sr/Ca ratios followed the approach outlined by Rosenthal *et al*. (1999) for precise element/Ca ratios using sector field ICP-MS. Average external precision (RSD) of Sr/Ca ratios in the laboratory standard was 0.2%.

Growth Rates

The external growth lines on *S. groenlandicus* are annual growth checks (Kim *et al*. 2003; this study - see Sr/Ca ratio results), and thus can be used to determine growth rates. Since we collected all clams live, each growth increment can be assigned to a specific calendar year. The distance between the ventral edges of successive growth lines along the line of maximum growth (shell height) was measured with a digital caliper to the nearest 0.01 cm. We do not include growth beyond the last growth line in our analyses because we do not know what portion of the present year this growth represents.

Shell growth of *S. groenlandicus* was modeled by fitting the von Bertalanffy growth function to age and shell height data for each clam using Minitab (Ver. 14.10, 1993). Bivalve growth declines with age, so growth increments within an individual and among individuals of different ages must be standardized before growth among years can be compared. We use the methods of Jones *et al.* (1989), employing the first derivative of the von Bertalanffy function with respect to time, to derive an ontogenetically-adjusted measure of annual growth:

$$d\mathrm{SH}_t / dt = k\mathrm{SH}_\infty e^{-kt}$$

where SH_t = shell height at age t, $d\mathrm{SH}_t / dt$ = modeled yearly change in shell height, t = age in years, SH_∞ = maximum, asymptotic shell height, k = growth constant.

After determining the average yearly changes in shell height based on growth data from all clams, we calculated the expected yearly increase in shell height for each clam for each year. We then divided the measured or observed shell growth for each year by the expected growth for that year to generate a standardized growth index (SGI). This removes the ontogenetic changes in growth and equalizes the variance for the entire series (Fritts, 1976). Once annual changes in shell growth were standardized, we calculated the mean SGI for each calendar year (because growth lines are deposited in winter, growth year is virtually synonymous with calendar year). The result is a record of year-by-year growth for the *S. groenlandicus* individual, with an SGI greater than one indicating a better than average year for growth, while a value less than one reflects a worse than average growth year.

Climatic and Meteorological Data

We examined relationships between clam growth and climate indices with potential influence on the region: the Arctic Climate Regime Index (ACRI), North Atlantic Oscillation (NAO) and Arctic Oscillation (AO). The AO is the first principal component of the sea level pressure field at latitudes > 20º N (Thompson and Wallace 1998, Stenseth *et al*. 2003), while the ACRI measures variations in Arctic Ocean and ice circulation based on the sea level height anomaly at the North Pole (Proshutinsky & Johnson, 1997; Johnson *et al.*, 1999; Proshutinsky, pers com. for updated index). The sea surface height anomaly at the North Pole is indicative of the predominant high-Arctic wind pattern. Data for the NAO, using the sea level pressure difference between Gibraltar and Southwest Iceland (Jones *et al*., 1997; Osborn *et al*., 1999), were obtained from (http://www.cru.uea.ac.uk/cru/data/nao.htm) and for the AO from (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html).

The Barents Sea temperature data (PINRO, Murmansk) is a time series of integrated ocean temperature from 0-200 m depth along the Kola transect, which runs from the Kola Peninsula northward to the ice edge along the 33° 30´ E meridian (Bochkov, 1982; Tereshchenko, 1997). We have used yearly means of Barents Sea temperature in our analysis.

Meteorological data were obtained from the four official weather stations around Svalbard (Longyearbyen, Ny Ålesund, Bear Island, and Hopen; Fig. 1) maintained by the Norwegian Meteorological Institute (http://eklima.met.no). Daily data of precipitation, pressure, and temperature were used to calculate seasonal and yearly averages.

Local ice conditions were estimated from imagery by the Nimbus-7 SMMR and DMSP SSM/I passive microwave satellite (Cavalieri *et al.* 1997). The spatial resolution of the satellite imagery is 25x25 km, and the cell used for the ice analysis is immediately northward of Rijpfjord proper. The temporal resolution is daily from 1988 to 2003 and every second day from 1978 to 1988. We calculated the ice free days per year as the number of days with ice cover <25% from 1 July to 30 October of a given year (the estimated period of active growth of *S. groenlandicus*). This measure relates closely (>90%) to ice free days in a calendar year and average yearly ice concentration. Data on total Arctic-wide spatial extent (km^2) of pack ice were obtained from the U.S. National Snow and Ice Data Center (http://www.nsidc.com/data/seaice_index/) (Fetterer& Knowles, 2002).

Statistical Analyses

We calculated Pearson correlation coefficients in order to determine basic pair-wise relationships between SGI and the environmental and physical variables. We compared annual means and also investigated the time-dependence between data in consecutive years, leading us to incorporate two data transformations: 2 year-running means were used to reduce the magnitude of interannual variability of both growth rate and environmental data, and a 1-year lag was used to account for the time for physical processes to be reflected in shell growth.

We used a general linear model to investigate the data at an individual clam level, firstly to identify predictors of *S. groenlandicus* growth, and secondly to test whether there were significant differences between the clams, included in the model as a random effect. To further justify pooling the growth rates of the sample of clams, we computed the

Cronbach α measure of reliability (e.g., Bland & Altman, 1997), for the available growth data on a common set of years available for all clams (1992-2002) to examine the homogeneity of the four clam growth rates. Once we established that the clams were a homogenous sample, we combined the clam data into an annual mean value as a more reliable indicator of annual clam growth rate. This mean was then used as a response variable in a multiple linear regression model, investigating relationships with all available annual predictor variables. In all analyses, we checked for serial correlation in the residuals, which should be absent to satisfy the assumptions of the regression model. Statistical analyses were done using Statistica (ver. 6) or SPSS (ver. 11.5.1).

Results

The clams collected were 20, 19, 18, and 11 years old, representing 68 years of growth data. We assayed Sr/Ca ratios from 440 samples spanning 16 growth increments, and 350 samples spanning 12 increments, in the 20 year-old (N1) and 19 year-old (N3) shells, respectively. The two Sr/Ca profiles were similar, with maximum values of between 3.5 and 4.5 mmol mol^{-1} in aragonite deposited during early life, and a minimum value of approximately 1.5 mmol mol^{-1} recorded as the individuals grew older (Fig. 3). There was clear periodicity in Sr/Ca ratios that corresponded to growth increments visible in the shells. The amplitude of Sr/Ca variation within an increment ranged from 2-2.5 $mmol.mol^{-1}$ in wide increments during the first 2-3 years of life to 1-1.5 mmol mol^{-1} as growth lines narrowed with age. Sharp declines in Sr/Ca ratios were invariably associated with the presence of a dark growth line, confirming the growth lines are winter growth checks.

The von Bertalanffy growth equation ($SH_t = 112.8(1 - e^{-0.032(t-t_0)})$ had an R^2 of 0.956 ($P \approx 0$), indicating that it was an excellent descriptor of these clams' growth. This allowed us to correct for changes in growth with age and confidently generate the expected growth for each calendar year (Standardized Growth Index = SGI).

SGI varied considerably over the 20 years of the data set (Fig. 4), with a range for individual clams between 0.27 in the poorest growth year (N1 in 2002) to 2.46 in the best growth year (N2 in 1996). The total population SGI ranged from 0.45 (2002) to 1.64 (1995). The differences in SGI's among years are clearly not random, but appear to follow a cyclic pattern with better growth in the mid-1990s bracketed by two poorer growth periods in the late-1980s and the early part of this century. Growth has declined steadily for the last 4 years of the series, with the worst growth in the last two years (2001, 2002).

To justify combining the growth rates for the individual clams into an average Cronbach's reliability coefficient was calculated for the years 1992 until 2002, for which we had data from all four clams. The value α=0.663 indicates a reasonably high level of reliability. Unless mentioned otherwise, the following results are for the average annual SGI values.

SGI is most highly correlated with precipitation on Hopen and the ACRI (Table 1). These positive correlations generally improve when running means are used instead of annual means for the environmental parameter and when the environmental data are lagged one year with respect to growth, growth corresponding better to the previous year's environmental data than the current year's. The ACRI was the only large-scale climate index related to clam growth (Fig. 5) and this correlation was very significant with a one-year lag and using the running mean (r = 0.671, P<0.001). Atmospheric pressure at Hopen

and Longyearbyen are also significantly correlated, in these cases negatively, with the SGI when a one year lag and the running mean of the environmental data are applied. Removal of the variability explained by the ACRI and a correlation analysis between the residuals and the SGI revealed significant negative correlations between the SGI and the Kola Sea temperature, precipitation at Ny Ålesund and air temperature in Longyearbyen.

Considering all explanatory variables and their lags as well as their running means as possible predictors, the best subset of predictor variables for the SGI which we identified are the ACRI averaged over the two years prior to SGI measurement (running mean with a 1 year lag) and the running mean (present and previous year) of precipitation at Ny Ålesund. The model is:

$$\text{Average SGI} = 1.715 + 0.319 \times \underset{\substack{\text{(2yr mean,}\\ \text{1yr lag)}\\ (P<0.00001)}}{\text{ACRI}} - 0.00183 \times \underset{\substack{\text{(2yr mean)}\\ (P<0.007)}}{\text{Ny Ålesund Precipitation}}$$

This model explains nearly 65% of the variability in the mean SGI ($R^2 = 0.649$). Although the individual variables are serially correlated, the residuals in the model are not autocorrelated (Durbin-Watson test statistic = 1.67), thus satisfying the assumption of the regression model. Fig. 6 shows the observed mean SGI plotted against the value predicted by our model, where the 45 degree line indicates perfect prediction. This shows that the model-generated SGI's closely track the measured values. The only significant residual is for the year 1991, which is over-predicted because of a 1-year drop in average SGI in an otherwise multi-year uptrend in SGI (Fig. 5). In other words, the serial autocorrelation breaks down in 1991.

Discussion

Growth of *S. groenlandicus* from northeast Svalbard is clearly related to the Arctic Climate Regime Index, a large scale arctic climate oscillation dependent on high-Arctic atmospheric circulation patterns (Proshutinsky & Johnson, 1997; Johnson *et al.*, 1999; Polyakov *et al*., 1999), through local environmental conditions. Fortunately, the *S. groenlandicus* growth we examined spanned large changes in the ACRI (from positive to negative phase and vice versa), offering us the opportunity to examine the response of this important member of the benthic community to large changes in climate. The response of *S. groenlandicus* to the ACRI and local conditions, however, was complex, including an apparent 1-year lag between physical forcing changes and biological response.

The use of bivalves as bioproxies for climate changes hinges on the ability to recognize annual markers in their shell. While it is generally assumed that lines visible on the external shell or internally in cross section are deposited annually, particularly at high latitudes, this assumption is not always tested (Andrews, 1972; Tallqvist & Sundet, 2000). When the periodicity of increments has been examined using changes in oxygen and carbon isotopes between presumptive annual lines (Witbaard *et al*., 1994; Heilmayer *et al*., 2003; Khim *et al*., 2003), or more rarely in polar environments, mark and recapture studies (Sejr *et al*., 2002), they have proved to be annual and are associated with a winter cessation of growth. In *S. groenlandicus* from the Chukchi Sea, $\delta^{18}O$ values vary systematically between growth lines with the highest values, reflecting the coldest temperatures, coincident with the dark lines on the shell, strongly suggesting the lines are deposited annually during winter (Khim *et al.*, 2003).

We found that Sr/Ca profiles also varied systematically between individual growth lines, with minimum values always associated with dark growth bands. Recent culturing studies have found that the Sr/Ca ratio is positively correlated with temperature in low-Sr aragonite from mollusk shells and fish otoliths (Zacherl *et al.*, 2003; Bath *et al.*, 2004), meaning that growth lines in *S. groenlandicus* from Rijpfjord are likely deposited during the winter. The within-year amplitudes of Sr/Ca variations we found are on the order of 50-100%, and are of a similar magnitude to those reported by Stecher *et al*. (1996) for the bivalve *Mercenaria mercenaria.* Thus, the results are clearly consistent with an annual deposition rate of growth lines in *S. groenlandicus* shells and justify use of external lines on the shells as annual markers.

Considerable effort has recently been directed towards understanding the relationships between climate variation and ecosystem structure and function. Climate oscillations and the associated changes in physical parameters such as temperature, water circulation, and ice cover have been shown to measurably influence marine ecosystems in the North Pacific, North Atlantic, and Southern Ocean by regulating the abundances of organisms at the base and upper levels of food webs (Fomentin & Planque, 1996; Stabeno & Overland, 2001; Hunt & Stabeno, 2002). *S. groenlandicus* growth is not strongly related to the North Atlantic Oscillation (NAO), the Arctic Oscillation (AO), which is itself related to the NAO (Deser, 2000; Hurrell *et al*., 2003), or the Barents Sea temperature (until after the effects of the ACRI are removed) (Table 1), which is influenced by incursions of the North Atlantic Current into the Barents Sea (Loeng, 1991), and only correlated with one of the environmental variables from locations outside the polar front (e.g. all locations except Hopen), atmospheric pressure at Longyearbyen. This pattern of relationships indicates that

we are measuring the response of the marine ecosystem to an exclusively Arctic phenomenon, rather than a temperate interaction with Arctic climate. Once the variability in the SGI attributed to the ACRI is removed, either in the multiple regression model or in the correlation analysis, precipitation at Ny Ålesund is related to the SGI.

The polar-scale effect of climate on *S. groenlandicus* growth, however, is not immediate or direct because variation in *S. groenlandicus* growth is best explained by the climate index one year earlier than the current years' growth (Table 1, regression model). Lagged response to climate oscillations are common in marine systems and can typically span many trophic levels (Post 2004) from benthic infauna (Tunberg & Nelson, 1998), including the bivalve *Arctica islandica* (Witbaard *et al*., 2003), to zooplankton (Pershing *et al*., 2004), fish (Ottersen *et al*., 2004) and birds (Thomson & Ollason, 2001). In the case of *S. groenlandicus*, the lag is probably because the local manifestations of the climate oscillation (i.e. precipitation) take a period of time to develop. Furthermore, there is likely an additional time lag associated with the biophysical coupling via physical constraints on food production, biological processes of consumption and assimilation as tissue and shell growth, and storage of energy as tissue from previous years.

Surprisingly, given the importance of ice in mediating environmental conditions in the Arctic, no measure of ice condition (summer ice free days, total arctic ice pack extent) was related to *S. groenlandicus* growth (Table 1). When the last 4 years of poor growth are removed from the analysis, however, there is a very strong, significant negative relationship between SGI and Arctic-wide extent of the pack ice (Fig. 7). It is remarkable that such a large scale measure of ice conditions as the extent of total pack ice across the Arctic explains over 50% of the interannual variability in the growth of *S. groenlandicus*.

This relationship disappears when the last 4 years are included in the analysis, suggesting a decoupling of the previously strong relationship between growth and ice conditions in the last 4 years.

The growth of *S. groenlandicus* is linked to the ACRI though the impact of the climate oscillation on the local physical conditions of precipitation and ice cover (Fig. 8). The integration of water column processes by long-lived Arctic benthos means that the effect of climate on *S. groenlandicus* growth may be direct or indirect, and the specific mechanisms of coupling between physical conditions and bivalve growth in Rijpfjord (Fig. 8) are not well understood. Variation in bivalve growth is typically best explained by variation in temperature and food (Buekema *et al.*, 1985; Beukema & Cadée, 1991; Jones *et al.*, 1989, Lewis & Cerrato, 1997; Dekker & Beukema, 1999; Witbaard *et al.*, 1997, 1999). Some of the best documented effects of climate oscillations on individuals, populations and benthic community structure are mediated through temperature (Kröncke *et al*., 1998; Ottersen *et al*., 2001; Hagberg *et al*. 2004). In late August when the clams in Rijpfjord were collected, the thermocline roughly coincided with collection depth (Fig. 2), indicting that the clams lived deep enough to experience relatively small differences in temperature over the year, meaning the temperature effects on growth will be limited and likely minor compared to other factors controlling food availability.

The growth of many polar benthic organisms appears to be food limited (Brockington & Clarke, 2001) and differences in growth among sites have been related to differences in food supply (Brey *et al*., 1995; Norkko *et al*., 2005). If the *S. groenlandicus* population in Rijpfjord is also food- rather than temperature-limited, processes regulating the quantity and quality of food reaching the bottom of the fjord will have a strong effect

on *S. groenlandicus* growth. In the absence of a strong temperature signal, variation in food quantity, and possibly quality, is the most probable explanation for interannual differences in *S. groenlandicus* growth in Rijpfjord. This is the same conclusion reached by Witbaard *et al*. (2003) for interannual variations in growth of *Arctica islandica* in the North Sea, and Sejr *et al*. (2004) for *Hiatella arctica* in east Greenland.

Precipitation is the only environmental variable that enters the multiple linear regression model as a negative relationship between SGI and precipitation at Ny Ålesund, and precipitation at Hopen is positively correlated with growth in current and previous years (Table 1) (precipitation at Ny Ålesund and Hopen are negatively correlated, though not significantly, hence their opposite relationships with the SGI). The effect of precipitation on *S. groenlandicus* growth could be due to direct or indirect effects and we have little data from Rijpfjord to help us interpret these relationships. The land around Rijpfjord is heavily glaciated and the un-glaciated areas are sparsely vegetated with nutrient poor soil, so spring runoff is unlikely to be laden with nutrients necessary to stimulate a phytoplankton bloom. Precipitation might also stabilize the water column, which has been shown to initiate a spring bloom in the Bering Sea (Stabeno & Overland, 2001) and west Greenland (Nielsen & Hansen, 1995), but is not necessary for a spring bloom to develop in the Rijpfjord system (Hegseth *et al*., 1995). Precipitation could affect the salinity of surface water and the abundance of herbivorous zooplankton, which are capable in Arctic fjords of consuming over 80% of annual primary production (Nielsen & Hansen, 1995) and indirectly influencing bivalve growth (Witbaard *et al*., 2003); a top-down rather than a bottom-up effect. It is also possible that precipitation is a reflection of storms, which may cause resuspension of settled phytodetritus, and in shallow enough

water, benthic microalgae, both of which could be consumed by *S. groenlandicus*, a positive relationship, or excessive wind might suspend bottom sediment clogging the gills of *S. groenlandicus* and resulting in lowered growth, a negative relationship. Without more information on environmental conditions in Rijpfjord and how they affect primary productivity and delivery of food to the benthos, we can do no more than speculate on the relationships between growth of *S. groenlandicus* and precipitation.

Perhaps the most intriguing aspect of the relationships between *S. groenlandicus* growth and environmental conditions is the decoupling which occurred during the last 4 years between ice cover and growth. Annual phytoplankton production in the Arctic is directly proportional to the length of open water (Rysgaard *et al*., 1999) and benthic biomass on Arctic shelves is, inversely related to ice cover (Ambrose & Renaud, 1995). In Rijpfjord, however, 3 weeks after the break-up of ice in 2003 during the period when the "spring" bloom would be expected, there was a very shallow mixed-layer depth (Fig. 2) and little suspended chlorophyll biomass in the water column (maximum 1 $\mu g\ L^{-1}$, E.N. Hegseth, unpub. data). Locally produced phytoplankton alone would appear to be insufficient to sustain the rich benthic communities observed in Rijpfjord, with infaunal benthic biomass of 130 g WW m^{-2} (M.L. Carroll, unpub. data) at 200 m depth adjacent to the bivalve collection site. Thus, we assume a significant amount of food must reach the bottom of Rijpfjord from non-local sources, with ice algae from ice flows episodically driven into the fjord by wind and advected phytoplankton being the most likely explanation (Carroll *et al*. in prep.). To the extent that the benthos in Rijpfjord is dependent on the advection of ice and associated ice algae for food, the recent reduction in summer ice north of Svalbard (Serreze *et al*., 2003;

http://nsidc.org/news/press/20050928_trendscontinue.html) or any change in wind or current patterns resulting in less ice entering the fjord would cause a reduction in this food source. Ice algae is a potentially important food source for the Arctic benthos (Ambrose *et al*., 2001 and references therein) including *S. groenlandicus* (McMahon *et al*., 2006). There may well be a balance between enough ice for ice algae-laden flows to be advected into Rijpfjord and too much ice reducing phytoplankton production in surrounding waters (the source for any advected phytoplankton) and limiting the movement of ice flows. There are as yet insufficient data to determine if there has been a fundamental shift in the biophysical coupling in Rijpfjord, but it is possible that the quality or quantity of food reaching the benthos has recently changed. This change could be a reflection of long term climate change in the Arctic that is now exerting an overriding effect on the benthos compared to local climatic conditions.

Bivalves have been used to reconstruct environmental conditions in ancient and modern environments for many decades. The long life of polar bivalves and the tight coupling between pelagic and benthic processes make them ideal candidates for monitoring climate change and for predicting the impact of global warming on Arctic marine ecosystems. Our results confirm the importance of *S. groenlandicus* as a biological proxy of climatic forcing on the marine ecosystem and are the first evidence of an Arctic-centered climate oscillation influencing marine benthic processes. Our results, however, do not reveal the proximate causes of variability in bivalve growth. To fully understand the response of *S. groenlandicus* and other bottom dwelling organisms to climate fluctuations, we need to better understand variation in the quality and quantity of food reaching the sea floor.

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Table 1: Pearson Correlations relating *S. groenlandicus* SGI to various environmental variables, 1983 - 2002. The first sets of two columns of coefficients are from annual data (temperature and pressure data used are annual means, precipitation is annual total sum) and 2-year running means of the annual data. The second set is from the environmental data being set back (lagged) by 1 year with respect to the growth data. The third set contains the correlations (1 year lag only) after the effects of the Arctic Climate Regime Index (2 year running mean, 1 year lag) have been removed. Significant correlations are shown in bold. The levels of the significant correlations are: * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

	Correlations with Average SGI				**Correlations with Residuals**	
	Present Year		**1 year lag**		**1 year lag**	
Environmental Variable	**Annual**	**Running Mean**	**Annual**	**Running Mean**	**Annual**	**Running Mean**
Kola Transect Sea Temperature	-0.032	0.008	0.045	0.033	-0.345	**-0.462***
Summer Ice Free Days in Rijpfjord	0.166	0.107	0.005	-0.050	-0.132	-0.145
Pack Ice extent March	-0.315	-0.232	-0.319	-0.137	-0.416	-0.422
Ny Ålesund Air Temperature	-0.020	-0.141	-0.204	-0.263	-0.409	-0.318
Ny Ålesund Pressure	-0.169	-0.349	-0.381	-0.428	0.044	0.202
Ny Ålesund Precipitation	-0.212	-0.257	-0.158	0.134	**-0.509***	-0.250
Longyearbyen Air Temperature	-0.002	-0.112	-0.181	-0.112	**-0.434***	-0.341
Longyearbyen Pressure	-0.198	-0.383	-0.408	**-0.455***	0.023	0.177
Longyearbyen Precipitation	0.047	0.181	0.199	0.389	-0.095	0.047
Hopen Air Temperature	-0.015	-0.114	-0.175	-0.199	-0.427	-0.362
Hopen Pressure	-0.216	-0.417	-0.432	**-0.451***	-0.055	0.150
Hopen Precipitation	**0.476***	**0.592****	**0.592****	**0.515***	0.341	0.244
Bear Island Air Temperature	-0.124	-0.167	-0.152	-0.196	-0.386	-0.354
Bear Island Pressure	-0.221	-0.374	-0.366	-0.364	-0.038	-0.175
Bear Island Precipitation	0.323	0.408	0.319	0.213	0.255	0.037
NAO Index (Annual)	0.025	0.106	0.140	0.209	-0.162	-0.148
NAO Index (Winter)	0.178	0.297	0.241	0.219	-0.081	-0.229
AO Index (Annual)	-0.021	0.129	0.233	0.332	-0.175	-0.219
AO Index (Winter)	0.242	0.358	0.322	0.368	-0.124	-0.223
Arctic Climate Regime Index	0.297	**0.522***	**0.492***	**0.671*****	-0.018	0.000

Figure Legends

Fig. 1. Map of the study region showing the Spitsbergen Archipelago, general current patterns, the locations of the meteorological stations (BI = Bear Island, HO = Hopen, LB = Longyearbyen, NÅ = Ny Ålesund), and the collection site of *Serripes groenlandicus* (Rijpfjord = RF). The polar front is the average location of maximum ice cover in late winter.

Fig. 2. Temperature and salinity profile from Inner Rijpfjord, near the location of bivalve collection on, 28 August 2003.

Fig. 3. Ratio of strontium to calcium in two *S. groenlandicus* shells (N1 and N3) from Rijpfjord. Samples were taken along each clam's height and are numbered from the umbo to the ventral margin. Triangles correspond to the location of dark growth lines visible on a shell's exterior.

Fig. 4. Standard Growth Index (±1 standard error of the mean) of the *Serripes groenlandicus* from Rijpfjord, Svalbard (Norway) collected live on 28 August 2003. Growth increments were calculated using external measurements and the von Bertalanffy equation to remove ontogenetic changes in growth. A standard growth index greater than 1.0 indicates greater than average growth while one less than 1.0 poorer than average. Growth was measured along the line indicated on the shell. The dark bands representing winter cessation of growth are visible on the shell.

Fig. 5. Temporal patterns of the Arctic Climate Regime Index, ACRI (gray bars), lagged one year, and *S. groenlandicus* SGI (line). The ACRI data are 2-year running means of raw data, while the SGI data are untransformed.

Fig. 6. Scatterplot of observed vs. modeled SGI from 1983-2002 with the growth years shown as data points. Line represents a perfect prediction by the model of actual growth rates of the *S. groenlandicus* population.

Fig. 7. Relationship between total Arctic-wide winter (March) sea ice extent (2 year running mean) and *S. groenlandicus* SGI from 1983 to 1998. (Ice data courtesy of National Snow and Ice Data Center, Boulder Colorado USA).

Fig. 8. Schematic representation of the Arctic Climate Cascade, where bivalve growth, and by inference, other ecosystem processes are linked to climatic forcing factors through variation in physical variables.

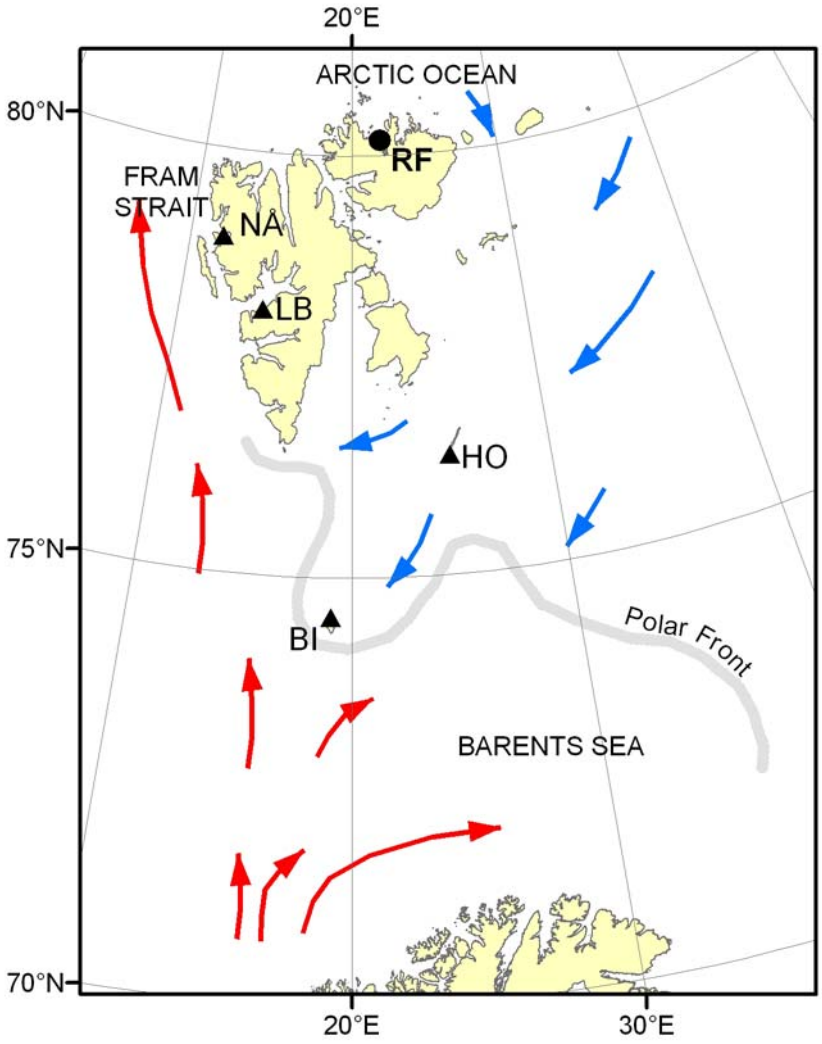
20°E
ARCTIC OCEAN
80°N
RF
FRAM
STRAIT
NA
LB
HO
75°N
BI
Polar Front
BARENTS SEA
70°N
20°E
30°E

Figure 1

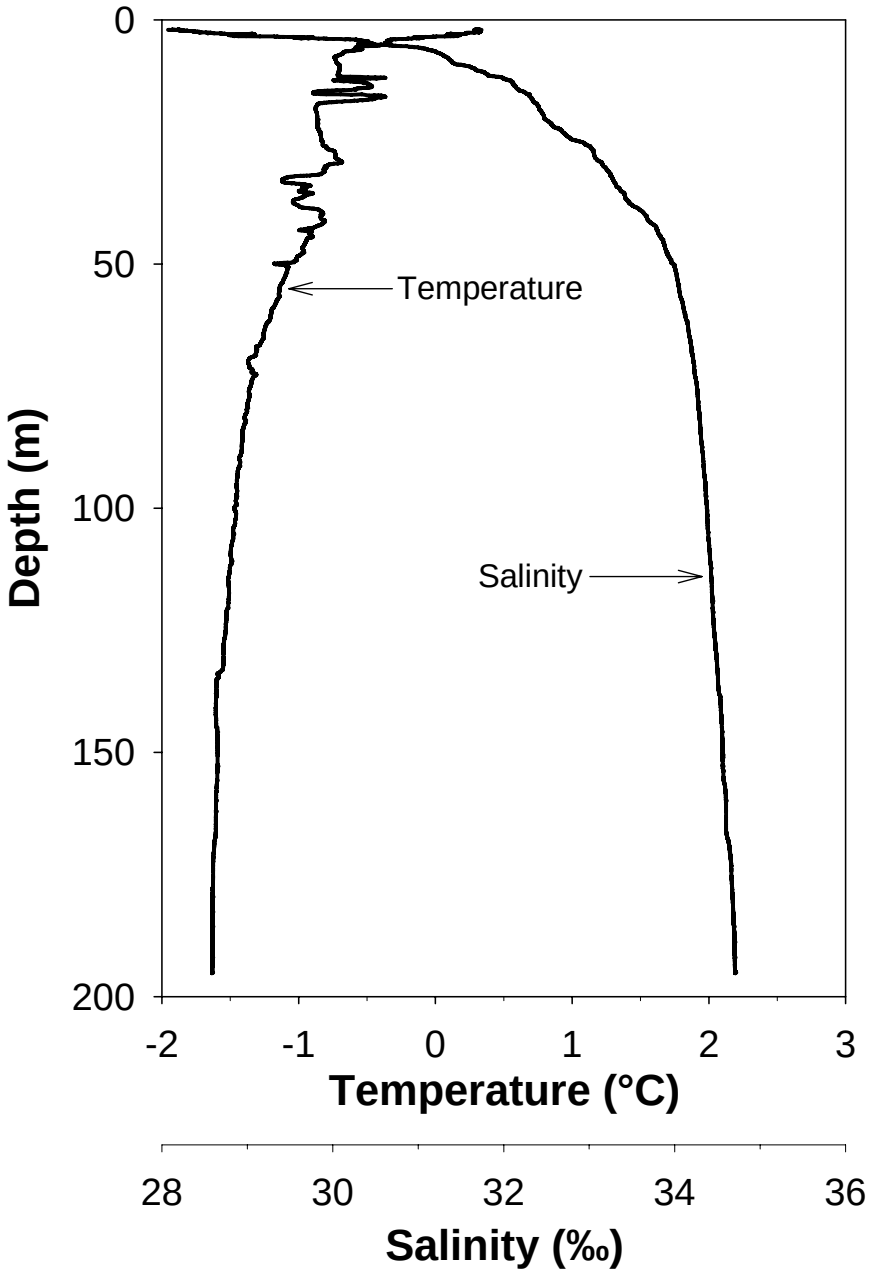
0
50
100
150
200
Depth (m)
Temperature
Salinity
-2
-1
0
1
2
3
Temperature (°C)
28
30
32
34
36
Salinity (‰)

Figure 2

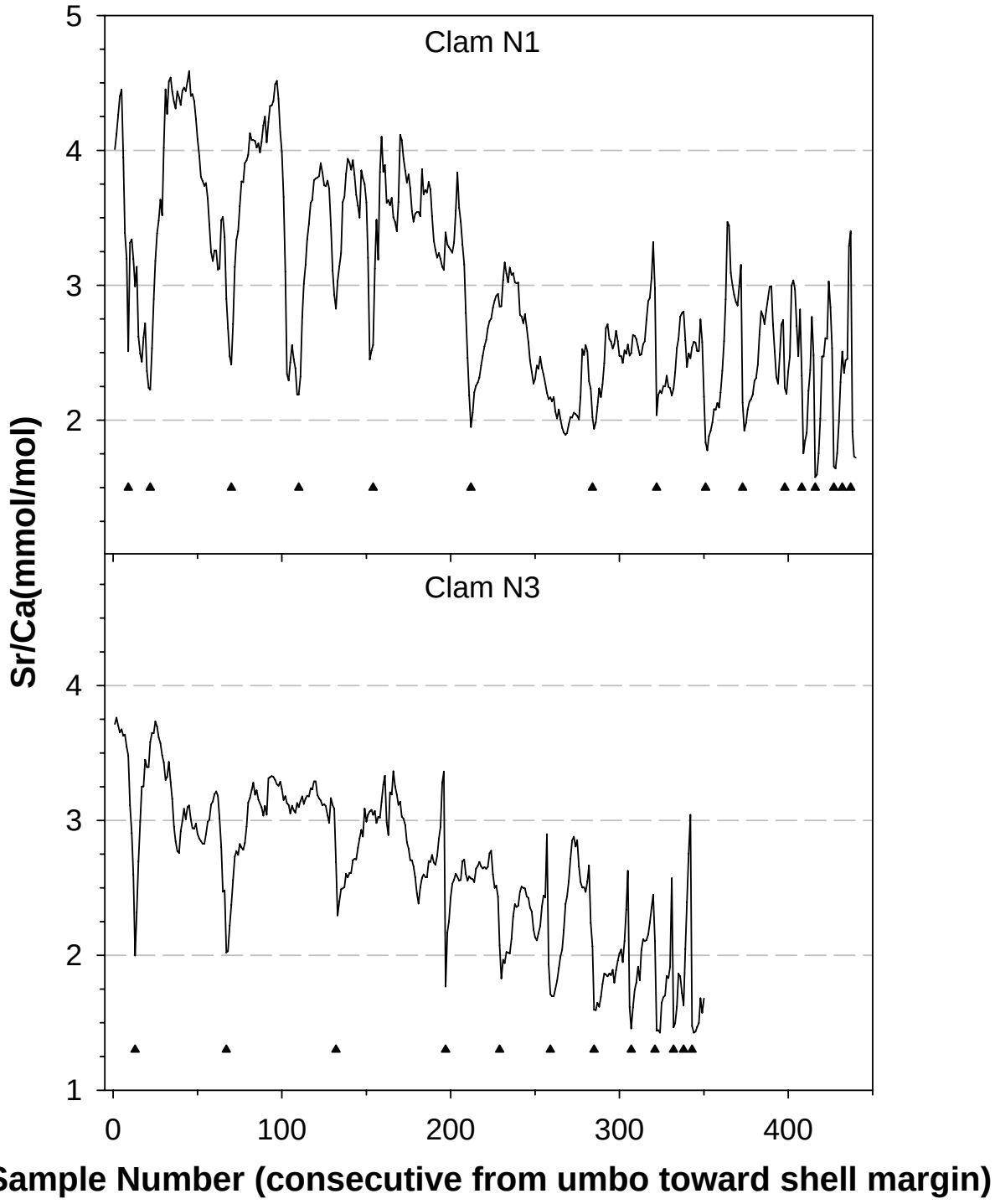
Clam N1
Clam N3
Sr/Ca(mmol/mol)
Sample Number (consecutive from umbo toward shell margin)
5
4
3
2
1
0
100
200
300
400

Figure 3

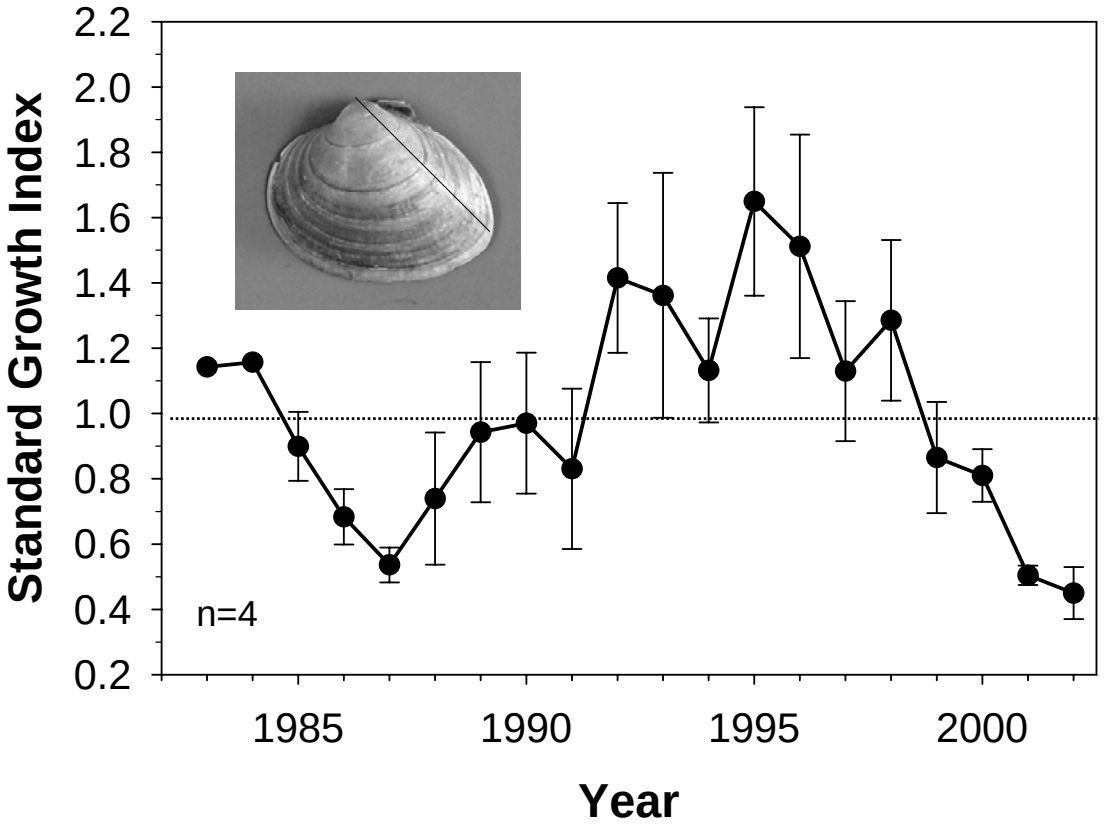
Standard Growth Index
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
n=4
1985
1990
1995
2000
Year

Figure 4

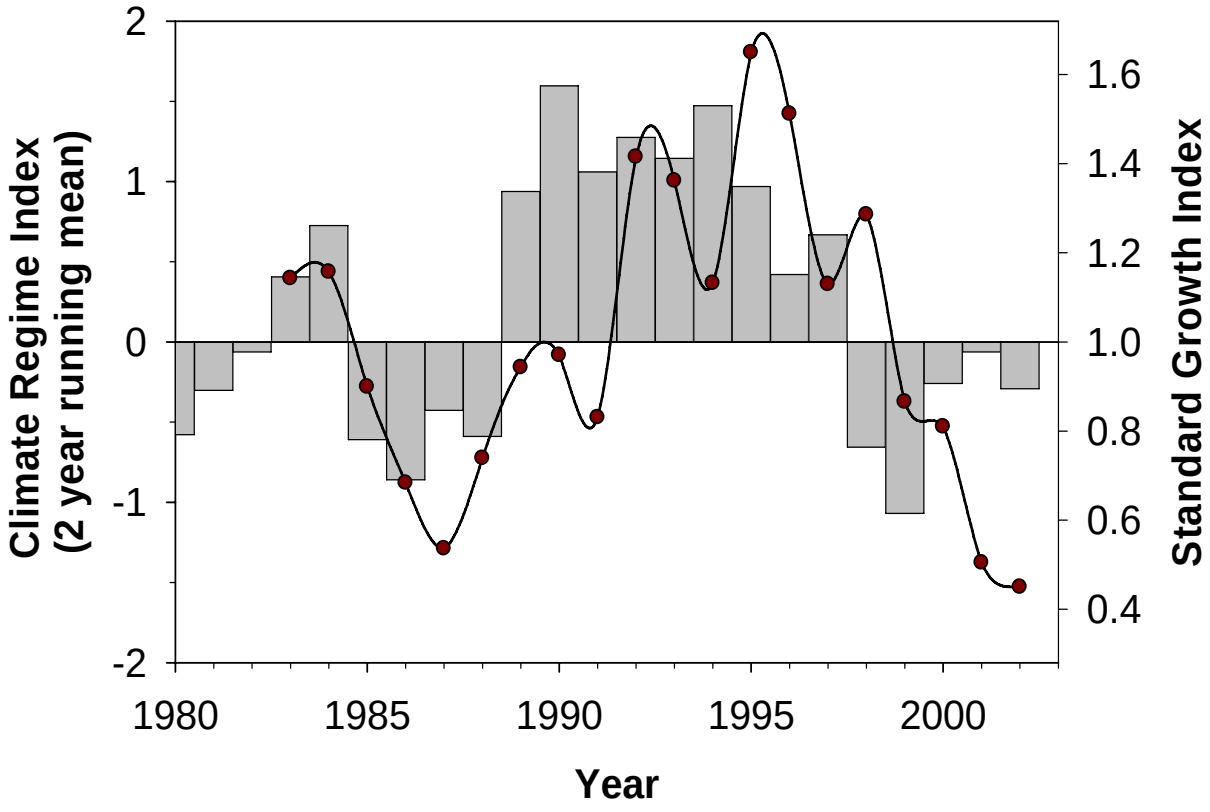
Climate Regime Index
(2 year running mean)
Standard Growth Index
Year
2
1
0
-1
-2
1.6
1.4
1.2
1.0
0.8
0.6
0.4
1980
1985
1990
1995
2000

Figure 5

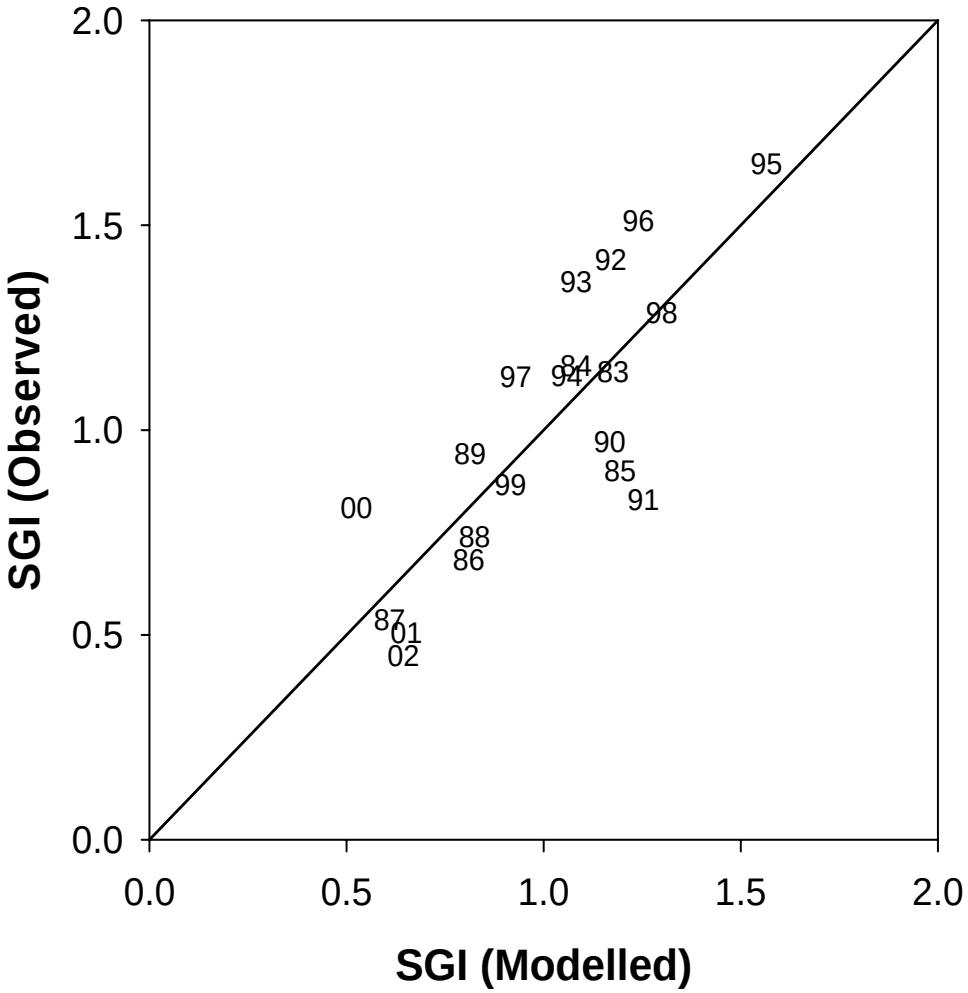
SGI (Observed)
SGI (Modelled)
2.0
1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
2.0
95
96
92
93
98
97
94
84
83
90
89
85
99
91
00
88
86
87
01
02

Figure 6

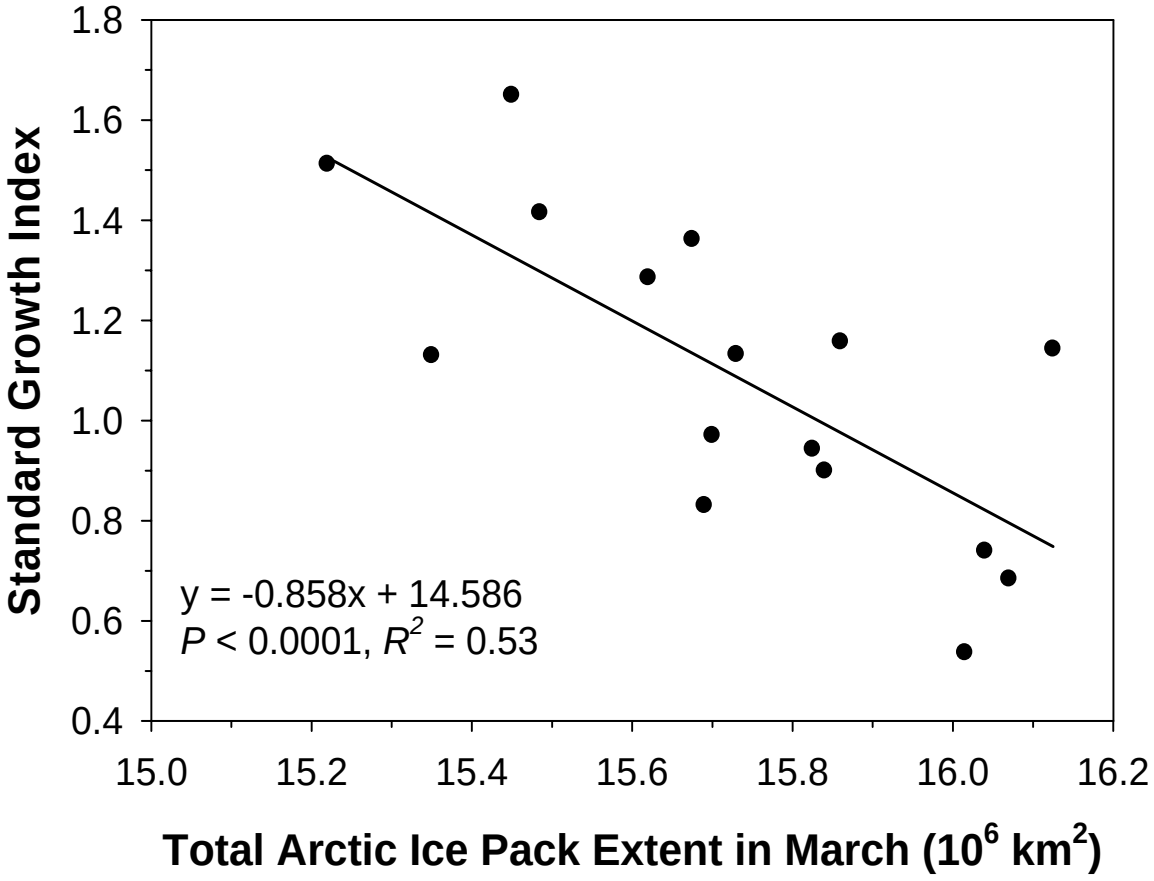
Standard Growth Index
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
y = -0.858x + 14.586
P < 0.0001, R2 = 0.53
15.0
15.2
15.4
15.6
15.8
16.0
16.2
Total Arctic Ice Pack Extent in March (10^6 km^2)

Figure 7

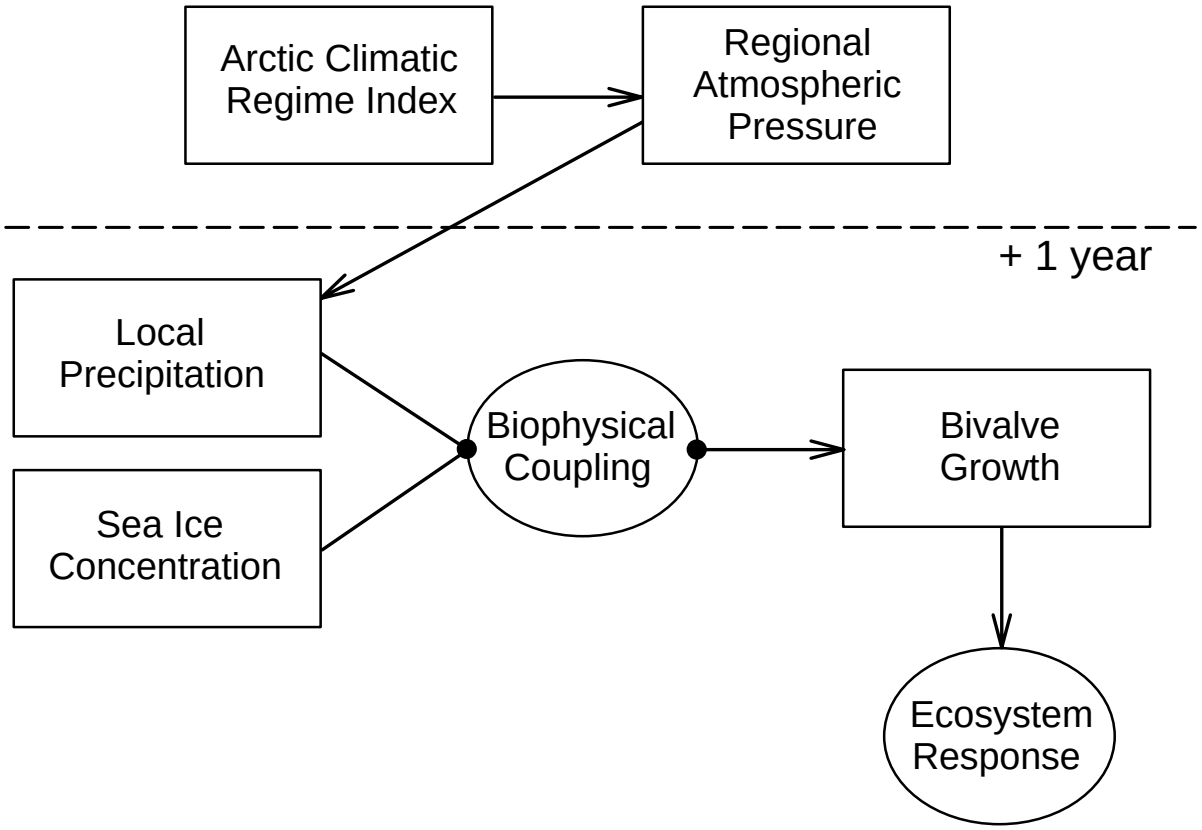
Arctic Climatic Regime Index
Regional Atmospheric Pressure
+ 1 year
Local Precipitation
Sea Ice Concentration
Biophysical Coupling
Bivalve Growth
Ecosystem Response

Figure 8